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Heat stress assessed using the temperature–humidity index and semen quality in Holstein-Friesian bulls: A review

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Abstract: Heat stress is an environmental factor affecting the reproductive performance of breeding bulls. In Holstein-Friesian cattle, which is the dominant dairy breed in intensive herds, elevated ambient temperature and humidity can negatively affect semen quality, production of freezable semen and fertility. To objectively assess heat stress, the temperature–humidity index (THI) is used in practice, which combines the effects of ambient temperature and relative humidity. This review article summarises current knowledge on the effect of high THI on the semen quality of Holstein-Friesian bulls, focusing on the physiological, cellular, and molecular mechanisms of the response to heat stress. An analysis of available studies shows that THI values ≥72 are associated with a decrease in sperm motility, viability, membrane integrity, and cryotolerance, as well as an increase in DNA fragmentation. Because spermatogenesis is continuous, high-THI events may affect germ cells at heat-sensitive developmental stages at the time of exposure. Their consequences may become evident in ejaculates collected during the following weeks, particularly approximately 30–60 days later, whereas the effect of thermal conditions on the day of collection is typically weaker but may still be detectable. Seasonal increases in THI result in a deterioration of post-thaw semen parameters. At the cellular level, thermal stress exerts its effects through oxidative stress, proteostasis disorders, disruption of the blood-testis barrier, and changes in the epigenetic programming of sperm. The article further discusses the influence of bull age, breed differences, and individual variability in sensitivity to heat stress.

Keywords: bull fertility; heat stress; dairy bull; semen quality; temperate climate zone

List of abbreviations

AI = artificial insemination; **ATP** = adenosine triphosphate; **BTB** = blood-testis barrier; **DFI** = DNA fragmentation index; **ERS** = endoplasmic reticulum stress; **EV** = extracellular vesicles; **HSP** = heat shock proteins; **miRNA** = microRNA; **Nrf2** = transcription factor regulating antioxidant response; **piRNA** = PIWI-interacting RNA; **PUFA** = polyunsaturated fatty acids; **ROS** = reactive oxygen species; **sncRNA** = small non-coding RNA; **THI** = temperature–humidity index; **tRNA** = transfer RNA; **UPR** = unfolded protein response

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INTRODUCTION

Climate change and the associated rise in global temperatures pose a fundamental challenge to contemporary animal production (Gloria et al. 2021). In cattle breeding, heat stress is identified as one of the key environmental factors limiting reproductive performance, as the male reproductive system exhibits sensitivity to increased thermal load (Al-Kanaan et al. 2015). The pathophysiological impact of elevated ambient temperature and humidity on bull fertility is primarily mediated by the disruption of thermoregulatory mechanisms, leading to testicular hyperthermia and subsequent sperm damage (Hansen 2009; Wettemann and Boehmer 2014). To objectively assess the combined effect of these stressors, the temperature–humidity index (THI) is utilised in practice (Al-Kanaan et al. 2015).

Ejaculate quality, which reflects the biological and fertilising capacity of sperm, is impaired under heat stress conditions by a complex cascade of events, including oxidative damage to cellular membranes, chromatin fragmentation, increased sperm apoptosis, altered hormone concentrations and disruption of proteostasis (Polsky and von Keyserlingk 2017; Staub and Johnson 2018; de Sousa Santos et al. 2022). The resulting changes in semen quality may become detectable only after a delay, depending on the stage of spermatogenesis affected. It should be noted that changes in semen quality are also the result of a complex interaction of genetic predispositions, animal age, nutrition, health status, and breeding management (Wettemann and Boehmer 2014; Llamas-Luceno et al. 2020).

Heat exposure and its reproductive consequences need to be considered in the context of the production system. Dairy bulls kept at artificial-insemination (AI) centres may be housed and monitored throughout the year, allowing environmental conditions and successive ejaculates to be evaluated. In AI programmes, heat-related changes in semen output and quality can affect the production of insemination doses, including their suitability for cryopreservation. Beef bulls used for natural mating may instead be exposed to pasture conditions during a defined breeding season, where shade, water availability, activity and opportunities for cooling influence the thermal load they experience. Under natural mating, semen quality is only one component of reproductive performance; mating behaviour and the heat exposure of cows also influence the observed pregnancy outcome. Because these settings are not directly interchangeable, this review focuses on semen quality in Holstein-Friesian bulls, particularly in AI systems, and uses evidence from other cattle breeds to explain mechanisms where appropriate (Kastelic et al. 2018; Morrell 2020).

The relationship between heat stress and bull reproductive performance is a complex issue that remains open to discussion even for regions with temperate climates (Johnson et al. 2000). Studies from temperate regions have nevertheless recorded a decrease in progressive motility and impaired sperm cryotolerance at higher THI levels, largely driven by oxidative stress and cellular damage. Consequently, cumulative or episodic heat stress remains a factor potentially affecting the final quality of insemination doses even in temperate climates (Valeanu et al. 2015; Sabes-Alsina et al. 2019).

This review therefore first describes the THI and its assessment, then summarises how the timing of heat exposure relative to spermatogenesis affects semen quality and the underlying cellular and molecular mechanisms, and finally discusses factors that modify the response of individual bulls.

TEMPERATURE–HUMIDITY INDEX (THI): METHODOLOGY AND ITS CATEGORIES

The THI is a key indicator for assessing the heat stress experienced by livestock. It combines the effects of ambient temperature and relative humidity in the environment (Coulter 2021). The thermal comfort zone may be defined as the range of environmental conditions in which an animal can maintain thermal balance without substantial activation of physiological or behavioural cooling mechanisms (Herbut et al. 2018; Ji et al. 2020).

A THI value of approximately 72 is widely used as a management-oriented threshold for the onset of heat stress in dairy cattle, particularly dairy cows. However, this value should not be regarded as a universal biological cut-off for bulls. In dairy cows, reported thresholds for physiological and production responses in temperate climates may occur at lower THI values, often in the range of approximately 60–68, whereas THI values above 75 are commonly associated with more severe heat load. In bulls, no single THI threshold has been consistently

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established. Reported associations between THI and semen traits vary according to breed, climatic region, housing conditions, acclimation, duration of exposure, THI calculation method, and the semen endpoint evaluated. Consequently, thresholds such as THI 68–72 should be interpreted as practical risk indicators rather than fixed limits of reproductive impairment in bulls (Al-Kanaan et al. 2015; Llamas-Luceno et al. 2020; Llavanera et al. 2021; Popovic et al. 2024; Savvulidi et al. 2025). At very high THI values, the physiological capacity for heat dissipation may become insufficient, particularly when exposure is prolonged or combined with restricted ventilation, limited water availability, or poor acclimation. This variability likely reflects differences in climatic conditions, housing systems, bull acclimation, breed, duration of heat exposure, and methodological approaches, including THI calculation and semen quality assessment (Sabes-Alsina et al. 2019; Bollwein and Malama 2023). Therefore, THI thresholds should be interpreted as management-oriented indicators rather than universal biological cut-off values, emphasising the need for long-term monitoring and population-specific validation.

Formula for calculating THI (McDowell 1972):

$$THI = (1.8 \times T + 32) - (0.55 - 0.005\,5 \times RH) \times \times (1.8 \times T - 26) \quad (1)$$

where:

T – air temperature in °C;

RH – relative humidity in %.

High THI values represent a complex stressor that combines the effects of hyperthermia with the body's limited ability to dissipate excess heat (Wettemann and Boehmer 2014; Morrell 2020). Threshold values are presented in Table 1. It is therefore essential to monitor THI values over the long term and systematically evaluate their relationship to reproductive parameters. To accurately determine THI values, data loggers for temperature and relative humidity are used, which enable long-term and continuous monitoring of microclimatic conditions in the barn. Sensors are typically placed directly within the housing areas, most often at a height of 1–2 m above the ground, i.e. approximately at the level of an adult animal's body. During installation, it is necessary to ensure that they are not exposed to direct sunlight or cold airflow from ventilation openings (Herbut et al. 2018).

The frequency of THI measurements depends on the purpose of monitoring and the type of equipment used. Most data loggers record data at intervals of 10–30 min, with the measured values subsequently aggregated into hourly or daily averages (Schuller et al. 2014). Some studies further utilise daily THI maximums or minimums, which allows for the capture of both short-term episodes of acute stress and longer-term thermal stress.

An alternative approach is to use data from the nearest weather stations, which allow for monitoring the broader environmental context and comparing results across multiple locations (Llavanera et al. 2021). However, direct measurement of the microclimate in the barn is generally considered more accurate because it reflects the actual conditions to which the animals are exposed.

TIMING OF HEAT EXPOSURE AND SEMEN QUALITY

Testicular thermoregulation, spermatogenesis and the time lag of heat effects

In bulls, normal sperm production requires testicular temperatures approximately 2–6 °C below core body temperature. Heat is dissipated through the thin, vascularised scrotal skin, while the testicular vascular cone provides counter-current heat exchange: the coiled testicular artery lies close to the veins of the pampiniform plexus, allowing arterial blood to cool before entering the testis. Scrotal

Table 1. Temperature–humidity index (THI) categories and recommendations for semen sampling

THI category	Interpretation	Recommendations for sampling
<68	comfort	standard mode
68–72	light load	morning sampling, slightly longer interval
≥72	medium load	morning sampling, longer interval, DNA fragmentation index/integrity check
≥78	heavy load	consider suspending sample collection

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heat loss and vascular heat exchange together help maintain the temperature gradient needed for spermatogenesis. Their effectiveness may be reduced when environmental heat load is high or sustained (Kastelic et al. 1997; Kastelic et al. 2018).

Spermatogenesis involves mitotic proliferation and differentiation of spermatogonia, meiosis of spermatocytes, and spermiogenesis, during which spermatids acquire the characteristic sperm head, acrosome and flagellum and undergo chromatin remodelling. Elevated testicular temperature can affect germ cells at these stages, with the nature and timing of subsequent changes in the ejaculate depending on the stage exposed and the duration of heating. This also distinguishes delayed effects on developing germ cells from effects on spermatozoa already present in the epididymis at the time of exposure (Kastelic et al. 2018; Staub and Johnson 2018).

Semen quality may begin to deteriorate approximately 1–2 weeks after heat exposure, with changes in motility and other functional parameters becoming more evident over the following 2–3 weeks. Recovery is usually observed before eight weeks after the heat challenge, although the duration depends on the intensity of exposure and the germ-cell stage affected. The precise timing depends on the intensity and duration of the thermal challenge and on the developmental stage of the germ cells affected (Wettemann and Boehmer 2014; Capela et al. 2022).

Given the duration of spermatogenesis and epididymal maturation, heat-induced effects may become detectable in the ejaculate over several weeks rather than immediately after exposure. Depending on the developmental stage of the affected germ cells, early changes may include morphological abnormalities, followed by impairment of membrane function and motility; DNA fragmentation may become more apparent later, around the fourth week in experimental models (Garcia-Oliveros et al. 2020; Capela et al. 2022).

After leaving the testis, sperm undergo a maturation process in the epididymis over approximately 9–11 days, which involves the remodelling of membranes and surface proteins. High THI alters the composition of epididymal secretions, increases membrane peroxidation, and reduces the integrity of the acrosome and plasma membrane, particularly following cryopreservation (Houston et al. 2018; Popovic et al. 2024).

Effect of high THI during spermatogenesis (30–60 days)

The period 30–60 days prior to ejaculate collection is considered the most sensitive, as this is when meiosis and the early stages of spermatogenesis occur (Llavanera et al. 2021). During spermatocytogenesis, germ cells undergo repeated divisions, ensuring the renewal of the stem cell population and the formation of spermatogonia, spermatocytes, and spermatids (Sharma 2018). The effects of heat stress manifest in several waves: THI values from the past 7–14 days correlate with the quality of maturing sperm (Al-Kanaan et al. 2015), whereas long-term exposure over 30–60 days interferes with sperm production in the seminiferous tubules (Llavanera et al. 2021). Climatic conditions during the 30–60-day window exhibit greater predictive power for parameters of motility, membrane integrity, and chromatin fragmentation than conditions prevailing on the day of collection (Llavanera et al. 2021).

When the physiological capacity for heat dissipation is exceeded, cellular homeostasis in both the testes and epididymis is disrupted. Mild to moderate heat stress can increase reactive oxygen species (ROS) production and oxidative DNA damage, including oxidised DNA bases and single-strand breaks, whereas more severe or prolonged exposure may impair mitochondrial function, plasma-membrane integrity and motility and increase the incidence of morphological abnormalities. The type and timing of abnormalities subsequently observed in the ejaculate depend on the developmental stage of germ cells affected by the thermal challenge. Observational and experimental studies, including data from European artificial insemination stations, show that high temperature and humidity in housing can adversely affect spermatogenesis and ejaculate quality (Valeanu et al. 2015; Kastelic et al. 2018; Garcia-Oliveros et al. 2020; Morrell 2020; Llavanera et al. 2021). In Holstein-Friesian bulls reared in a temperate climate, reduced sperm viability and a lower proportion of implanted blastocysts following *in vitro* fertilisation have been repeatedly observed during periods of high THI, reflecting the high sensitivity of meiotic spermatocytes and early spermatids (Morrell 2020).

Effect of high THI measured on the day of collection

Exposure to high THI on the day of collection cannot substantially alter spermatogenesis that has

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already taken place, but it may affect the handling and functional performance of mature spermatozoa stored in the epididymis. The immediate effect should therefore be distinguished from delayed effects caused by heat exposure during germ-cell development (Garcia-Oliveros et al. 2020; Morrell 2020). In field studies, associations between the THI on the collection day and semen quality may also reflect cumulative exposure during the preceding days; consequently, the collection-day THI should not be interpreted in isolation (Morrell 2020).

Popovic et al. (2024) reported associations between THI and the production and quality of native semen and discussed preventive measures, including the selection of heat-tolerant bulls, air-conditioning of collection areas, and adjustments to the collection schedule.

Evidence from temperate climate conditions

Under Czech conditions, monitoring at an artificial-insemination station did not detect a consistent adverse association between THI and ejaculate quality, probably because bulls remained within the thermal comfort range for most of the year. A weak positive correlation was nevertheless observed between the number of days with THI > 70 during spermatogenesis and the proportion of viable sperm. This association should not be interpreted as evidence that moderate heat exposure improves sperm viability. Rather, it may reflect the limited number of high-THI days, restricted variation in thermal load, seasonal or management-related confounding, and the adaptive capacity of bulls maintained under controlled station conditions (Savvulidi et al. 2025).

The apparent inconsistencies among studies should not be interpreted as contradictory evidence but rather as an indication of the multifactorial nature of heat stress. Besides ambient temperature and humidity, semen quality is influenced by genetic background, nutritional status, health, housing, collection management, and individual adaptive capacity (Wettemann and Boehmer 2014; Morrell 2020). Consequently, bulls exposed to similar THI values may exhibit markedly different reproductive responses. Future investigations would benefit from greater standardisation of THI assessment, consistent characterisation of exposure periods relative to spermatogenesis, and harmonised laboratory methodologies for semen evaluation. Such standardisation would substantially improve comparisons among studies and facilitate the identification of biologically meaningful thresholds for reproductive management (Al-Kanaan et al. 2015; Llamas-Luceno et al. 2020).

CELLULAR AND MOLECULAR MECHANISMS OF HEAT-INDUCED DAMAGE TO SPERM

Hyperthermia at high THI triggers a cascade of molecular changes involving increased production of ROS, a decrease in mitochondrial membrane potential, and disruption of acrosome integrity, leading to reduced progressive motility and cryotolerance of sperm. Long-term exposure further manifests as chromatin condensation disorders and an increase in the DNA fragmentation index (DFI) (Wettemann and Boehmer 2014; Polsky and von Keyserlingk 2017). In testicular tissue, high THI activates a complex network of stress responses, including the regulation of proteostasis, redox balance, and inflammatory pathways, particularly via heat-shock proteins (HSPs), the unfolded protein response (UPR/ERS), and the Nrf2 transcriptional axis. These processes influence the function of the blood-testis barrier, steroidogenesis, and sperm maturation and are accompanied by changes in the transcriptome and proteome, as well as more stable epigenetic modifications, such as changes in DNA methylation, histone marks, and the profile of small non-coding RNAs (sncRNAs) (Aravindh et al. 2025; Jianfang et al. 2025; Zhang and Sirard 2026).

Oxidative stress and sperm membranes

The main mediator of sperm damage is oxidative stress. Hyperthermia increases ROS production in both germ and somatic cells of the testes and in differentiated sperm, leading to lipid peroxidation of flagellar membranes rich in polyunsaturated fatty acids (PUFAs), a decrease in adenosine triphosphate (ATP) production, and impaired motility. The timing of abnormalities detected in successive ejaculates after testicular heating should be distinguished from the mechanisms of damage within an individual spermatozoon. In the former, the appearance of particular morphological defects depends on which germ-cell stages were exposed; in the latter, excess reactive oxygen species can affect membrane lipids, proteins, mitochondrial function and DNA through interacting processes,

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without a fixed sequence in which a visible morphological defect must precede molecular damage (Bollwein and Bittner 2018; Kastelic et al. 2018; Garcia-Oliveros et al. 2020). Heat stress during epididymal maturation or *in vitro* capacitation accelerates changes in the sperm plasma membrane, including cholesterol efflux and alterations in Ca^{2+} signalling, leading to premature capacitation and early acrosomal reaction. This premature activation reduces sperm fertilisation capacity, as they arrive at the oocyte in a functionally exhausted state. In cattle, high-temperature-induced acrosomal reaction has also been associated with changes in calmodulin-dependent protein kinase II (CaMKII) localisation (Wettemann and Boehmer 2014; de Sousa Santos et al. 2022).

Proteostasis, heat-shock proteins and antioxidant defence

Heat-shock proteins (HSPs) act as molecular chaperones that support protein folding and limit the aggregation of heat-damaged proteins. However, the testicular heat-shock response is cell-type and protein-specific: inducible HSPs and constitutively expressed proteins involved in normal spermatogenesis should not be treated as interchangeable markers of heat exposure. When thermal injury is sufficiently severe, susceptible germ cells may undergo apoptosis despite the presence of cellular stress-response pathways; HSP induction alone does not establish that those pathways prevented cell death (Kim et al. 2013; Jianfang et al. 2025).

HSP70-2 has important functions in spermatogenesis and sperm function, but its detection alone should not be considered a specific indicator of recent heat exposure (Kim et al. 2013; Rosyada et al. 2022). Its abundance in ejaculated sperm may nevertheless be associated with sperm functional status and cryotolerance. Pardede et al. (2023) reported that higher HSP70 abundance was associated with more favourable post-thaw semen parameters. This finding should be interpreted as an association with cellular protection and sperm resilience rather than as a specific diagnostic indicator of recent environmental heat exposure.

Prolonged exposure to elevated temperatures leads to endoplasmic reticulum stress, which activates the unfolded protein response (UPR). This response temporarily supports the maintenance of proteostasis; however, under persistent thermal stress, it can transition into a pro-apoptotic phase characterised by increased degradation of spermatogonia and spermatocytes (Jianfang et al. 2025). Considerable changes in the proteome and chaperones have been observed in testicular tissue and sperm, and these changes affect sperm motility and their interaction with the *zona pellucida* (Wettemann and Boehmer 2014).

Simultaneously, antioxidant pathways are activated, particularly via the nuclear factor erythroid 2-related factor 2 (Nrf2) axis, which mitigates damage to cell membranes and DNA caused by ROS. However, in the absence of an adequate antioxidant response, sperm damage accumulates, manifesting as reduced motility and lower resistance to cryopreservation (Aravindh et al. 2025).

Blood-testis barrier, Sertoli and Leydig cells

Sertoli cells and the blood-testis barrier (BTB) are among the structures that are extremely sensitive to thermal stress. Both acute and chronic hyperthermia destabilise the tight junctions of Sertoli cells, including the proteins occludin, claudin-11, and ZO-1, thereby increasing the permeability of the BTB and limiting the trophic support of spermatogenesis. In mouse models heat-induced stress granules in Sertoli cells are associated with reversible BTB dysfunction and increased permeation of small molecules (Zhao et al. 2024). Long-term exposure to environmental stressors, particularly high ambient temperatures exceeding 32 °C (or THI values >72), leads to an increase in intratesticular temperature by 1.5–2 °C. This condition is associated with abnormalities in testicular ultrastructure and mitochondrial metabolism, which further exacerbates the disruption of BTB integrity (Jiang et al. 2025). Concurrently, steroidogenesis in Leydig cells may be disrupted and androgen concentrations may decrease, which further inhibits spermatogenesis (Ji et al. 2020). BTB and sperm proteome alterations may also contribute to premature capacitation and reduced fertilisation competence (Wettemann and Boehmer 2014; Polsky and von Keyserlingk 2017).

Chromatin condensation and DNA integrity

Heat-associated oxidative stress can damage sperm DNA through several related, but distinct, mechanisms. Reactive oxygen species may oxidise DNA bases, particularly guanine, producing 8-hydroxy-2'-deoxyguanosine (8-OHdG), a marker of oxidative DNA damage. Oxidised bases do not themselves demonstrate that a DNA strand has

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broken. Processing of these lesions by base-excision repair generates intermediates that require further repair; additionally, direct oxidative attack on the DNA backbone can produce strand breaks. Developing germ cells retain DNA-repair mechanisms, whereas the capacity of mature spermatozoa to complete repair is limited. Consequently, unresolved lesions may persist in sperm chromatin, particularly where chromatin remodelling or condensation has been disturbed (Bollwein and Bittner 2018; Houston et al. 2018).

These endpoints should also be distinguished analytically. Immunodetection of 8-OHdG measures oxidised DNA bases, whereas sperm chromatin structure assays report susceptibility of chromatin to denaturation as a DFI; the two results are not interchangeable. An antibody-based OXYDNA assay combined with flow cytometry has, for example, been used to evaluate 8-OHdG in bull spermatozoa, alongside a separate sperm chromatin structure assay (Carreira et al. 2017). In that study, however, the comparison concerned bull age rather than experimental heat exposure. Heat-induced oxidative DNA lesions have also been demonstrated in an experimental mouse model, which supports the proposed mechanism but should not be presented as direct evidence for a particular THI threshold in Holstein-Friesian bulls (Houston et al. 2018).

Epigenetic remodelling of sperm

In addition to direct oxidative lesions, changes in spermatogenic RNAs and epigenetic marks have been described, which may persist even after the resolution of heat stress (Sabes-Alsina et al. 2019; Evans et al. 2021).

DNA methylation. Review studies in livestock indicate that heat stress considerably affects the CpG methylation profile of genes associated with heat tolerance, immune response, apoptosis, and energy metabolism. These changes may persist into mature sperm and influence early embryogenesis. DNA methylation thus represents a key mechanism linking environmental conditions, as expressed by THI values, to the organism's phenotypic response and potential adaptation to high temperatures (Aravindh et al. 2025).

Histone marks and residual histones. Despite extensive protamination, bull sperm retain some histones bearing regulatory marks, such as H3K4me3 and H3K27me3. These histone modifications may be rearranged due to high temperature and subsequently influence the embryo's transcriptional competence after syngamy (Jianfang et al. 2025). This concept is also highlighted in a recent review focusing on epigenetic markers of sperm from bulls of dairy breeds, which proposes the use of histone marks in combination with other epigenomic layers for fertility prediction (Zhang and Sirard 2026).

Sperm-borne small non-coding RNAs and epididymal "reprogramming". Immature sperm contain a broad spectrum of small non-coding RNAs (sncRNA), including miRNAs, piRNAs, and tRNA fragments, whose profile is remodelled during passage through the epididymis via epididymal extracellular vesicles (EVs) (Zhang and Sirard 2026). Heat stress alters the composition of sncRNA in both the testes and epididymis, and these changes can be transmitted to the zygote and affect early embryogenesis as well as overall herd fertility (Aravindh et al. 2025).

Inter- and transgenerational aspects. Epigenetic layers of sperm, including DNA methylation, histone variants, and sncRNA, can mediate the transmission of environmentally acquired traits to offspring. These epigenetic features may represent promising biomarkers of the long-term consequences of heat stress in breeding bulls, although their value as direct selection criteria remains to be validated (Zhang and Sirard 2026).

FACTORS MODIFYING THE RESPONSE TO HEAT STRESS

Bull age, collection order and breed

Ejaculate production parameters, particularly volume and sperm concentration, are strongly influenced by bull age and collection order, i.e. whether the sample is the first or a subsequent ejaculate obtained from the same bull during a collection session. These factors should therefore be accounted for when statistically evaluating the effect of high THI (Llamas-Luceno et al. 2020).

The response to heat stress is further modified by breed differences. A genetic predisposition to higher heat tolerance has also been confirmed in relation to ejaculate volume (Tohura et al. 2018). Differences in the response to thermal load have been reported between Belgian Blue and Brown Swiss bulls. In a longitudinal comparison, increasing THI was associated with reductions in semen

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volume, sperm concentration, total sperm number, motility, membrane integrity, and normal morphology in Belgian Blue bulls, whereas these associations were limited or absent in Brown Swiss bulls (Gloria et al. 2021). The observed differences may reflect breed-specific variation in thermoregulation, metabolism, body conformation, and individual adaptive capacity. One explanation may also be the different production type, with the Belgian Blue being a typical beef breed, while the Brown Swiss is a dairy or dual-purpose breed.

Individual variability and genetic background of heat sensitivity

Individual bulls may differ substantially in their semen response to high THI. Al-Kanaan et al. (2015) reported a genotype × environment interaction, indicating that genetic values estimated under thermoneutral conditions may not fully predict performance under heat stress. Similarly, heat-sensitive and heat-tolerant groups have been described on the basis of longitudinal semen-quality records (Netherton et al. 2022). These observations indicate that individual resilience may modify the response to heat stress; however, the present review does not address genomic selection or the implementation of heat-tolerance traits in breeding programmes.

CONCLUSION AND PRACTICAL RECOMMENDATIONS

This review summarises current knowledge on the effects of heat stress on the reproductive performance of bulls and highlights THI as a practical indicator for assessing the risk of thermal stress. Because spermatogenesis is continuous, a high-THI event may affect germ cells that are at heat-sensitive developmental stages at the time of exposure. The consequences of such exposure may subsequently become evident in ejaculates collected over the following weeks, particularly approximately 30–60 days later. Therefore, whenever bulls experience elevated THI, semen collected during the subsequent 30–60-day period should be monitored closely. Heat stress may impair sperm motility, membrane integrity, chromatin stability, and cryotolerance through a complex network of cellular and molecular mechanisms, including oxidative stress, disruption of proteostasis, impairment of the blood-testis barrier, and epigenetic remodelling. Bulls differ in their sensitivity to heat, which is influenced by age, breed, and individual genetic background.

From a practical perspective, systematic monitoring of barn microclimate, appropriate adjustment of semen collection schedules during periods of elevated THI, and comprehensive semen quality assessment, including membrane integrity and DNA fragmentation analyses, should become integral components of reproductive management.

Despite substantial advances in this field, important knowledge gaps remain. Differences in THI calculation, exposure assessment, semen evaluation protocols, and experimental design currently limit direct comparisons among studies and hinder the establishment of universally applicable biological thresholds. Furthermore, variation in breed-specific responses, management systems, and the scarcity of long-term longitudinal studies complicate the interpretation of existing evidence. Future research should therefore prioritise methodological standardisation, longitudinal phenotyping under commercial conditions, and the integration of environmental, phenotypic, and molecular (including epigenetic) data. Rather than identifying a single universal THI threshold, the next generation of studies should focus on developing predictive models that account for cumulative heat load, individual bull resilience, and genotype × environment interactions, thereby enabling more precise reproductive management of bulls under heat stress.

Conflict of interest

The authors declare no conflict of interest.

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